

Observations on the structure of the mandibular gnathobase in some American *Mesocyclops* (Copepoda: Cyclopidae)

E. Suárez-Morales, M. A. Gutiérrez-Aguirre, and M. Elías-Gutiérrez

El Colegio de la Frontera Sur (ECOSUR) Unidad Chetumal. A.P. 424. Chetumal, Quintana Roo 77000. Mexico, e-mail: esuarez@ecosur-qroo.mx

Abstract.—The mandibular edge of males and females of several American species of the cyclopoid genus *Mesocyclops* was examined. The general structure, arrangement, and size of teeth was assessed for each species and shown to be variable among them. We used a modified version of a previous index, the Gnathal Index (GI) plus the Mandibular Size Index (MSI), and the Mandibular Power Index (MPI) which, together are expected to 1) provide a quantitative measure of morphologic variation amongst species and 2) suggest the feeding habits of these species. All species showed different values in terms of teeth number, size, and arrangement, as indicated by results of these indices. Known predatory species (i.e., *M. edax*, *M. longisetus*, and *M. aspericornis*) showed high values of MSI and MPI. The MSI values were positively correlated to the total body length. Our data suggest a predatory capability for these two species. *Mesocyclops yutsil*, *M. reidae*, and *M. chaci* had the lowest MPI and MSI values; they represent a group that probably are detritivores. The remaining species, all with lower MPI values, are probably omnivores. For the species examined here, most males are smaller than females but their mandibles tend to be similar in relative size and structure. Experimental observations support our conclusions about the predatory forms. Feeding experiments are needed to determine the limits of these indices for most species in the second and third groups.

Knowledge of the mandibular structure in the species of the freshwater copepods genus *Mesocyclops* is limited to the basic descriptions. There are no previous comparative studies about the morphology and specific variation of the mandible structures in freshwater copepods. Mandibles, together with other cephalic appendages, are directly involved in food handling and ingestion; hence, different feeding habits may be expected to correlate with particular mandible types.

Most species of the freshwater cyclopoid genus *Mesocyclops* are omnivorous. However, the role of some *Mesocyclops* as predators of mosquito larvae and consequently as biological controls has been studied for several years in the neotropical and nearctic

regions (Marten 1989; Marten et al. 1989, 1994a, 1994b), and in several Asian countries (Sinh Nam 2000) suggesting that these species may be carnivores. However, there are no surveys dealing with the morphological bases of their capacity for carnivory in terms of the structure and size of their mouthparts, particularly of their mandibles. The morphological structure of marine calanoid copepod feeding appendages (i.e., the cutting edges of the mandible or the structure of the maxillar setae) is a tool useful to infer their feeding habits (Itoh 1970). This aspect has not been explored in freshwater cyclopoid copepods, a group found in a wide range of continental environments and with different feeding habits.

There are ten species and one subspecies

Table 1.—Gnathal Index (GI), Mandibular Size Index (MSI), and Mandibular Power Index (MPI) obtained from the analysis of females and males of some American species of *Mesocyclops*. Species arranged alphabetically; numbers between parentheses indicate the rank of the MPI value.

Species	GI	MSI	MPI
<i>M. aspericornis</i> (Daday, 1906) (♀)	67.9	4.16	282.4 (2)
<i>M. brasiliensis</i> Kiefer, 1936 (♀)	63.6	2.79	177.4 (10)
<i>M. brasiliensis</i> (♂)	60.6	2.92	176.9 (11)
<i>M. chaci</i> Fiers, 1996 (♀)	51.2	2.05	104.5 (15)
<i>M. edax</i> (Forbes, 1891) (♀)	82.4	4.51	371.6 (1)
<i>M. evadomingoi</i> Gutiérrez-Aguirre, 2001a (♀)	75.6	2.41	182.1 (8)
<i>M. longisetus</i> s.str. (Thiébaud, 1912) (♀)	62.5	3.26	203.7 (5)
<i>M. longisetus curvatus</i> Dussart, 1987 (♀)	73.2	2.54	186.4 (7)
<i>M. pescei</i> Petkovski, 1986 (♀)	85.0	2.56	217.5 (4)
<i>M. pescei</i> (♂)	63.1	2.79	176.1 (12)
<i>M. residua</i> Petkovski, 1986 (♀)	75.0	2.02	151.5 (13)
<i>M. reida</i> (♂)	80.2	2.23	178.4 (9)
<i>M. thermocycloides</i> (Harada, 1931) (♀)	72.9	2.63	191.7 (6)
<i>M. thermocycloides</i> (♂)	87.0	2.79	234.8 (3)
<i>M. yutsil</i> Reid, 1996 (♀)	77.9	1.92	149.5 (14)

of *Mesocyclops* known to be distributed in Mexico (Suárez-Morales & Reid 1998, Gutiérrez-Aguirre & Suárez-Morales 2001a, 2001b; Fiers et al. 2000), representing close to 60% of the species currently known from the neotropics (Gutiérrez-Aguirre & Suárez-Morales 2001b). In this work, analyzes the structure of the mandibular edge of ten species and one subspecies of *Mesocyclops*, all of them known to be distributed in Mexico and Central America, and some found also in North America. The mandible edge structure and relative size are determined for the species of *Mesocyclops* examined, and variations among species are discussed in relation to their feeding habits. A quantitative aspect of this question is analyzed through different indexes, one of them derived from a formula first proposed by Itoh (1970) for the evaluation of the mandible structure of marine calanoid copepods.

Methods

Specimens were obtained from field collections of zooplankton in different freshwater environments of Mexico. The methods of collection and sampling sites in Mexico are described in Suárez-Morales et al. (1996) and in Gutiérrez-Aguirre and

Suárez-Morales (2001a). Additional type and non-type material was requested on loan to different museums harboring collections of American *Mesocyclops*, the National Museum of Natural History, Smithsonian Institution at Washington, D.C. (USNM), the Museum National d' Histoire Naturelle, Paris (MNHN-Cop), and El Colegio de la Frontera Sur, Unidad Chetumal, Chetumal, Mexico (ECO-CHZ) (see Suárez-Morales & Gutiérrez-Aguirre 2001). Female specimens of eleven species or subspecies plus males of four species of *Mesocyclops* recognized in Mexico and Central America were analyzed (see Table 1). Examination followed dissection of the mandibles and included camera-lucida illustrations of the mandibular edge detailing the teeth width, height, number, and separation.

Mandibular morphology.—In general, the morphological interpretation proposed by Huys & Boxshall (1991) was followed. The gnathobase is a ventral extension of the coxa; it has a variable number of non-articulation elements, that are the teeth. The mandible edge bears a proximal seta and in some cases an inner, flexible setiform extension (named “inner” proximal tooth). Both elements, the proximal seta and the

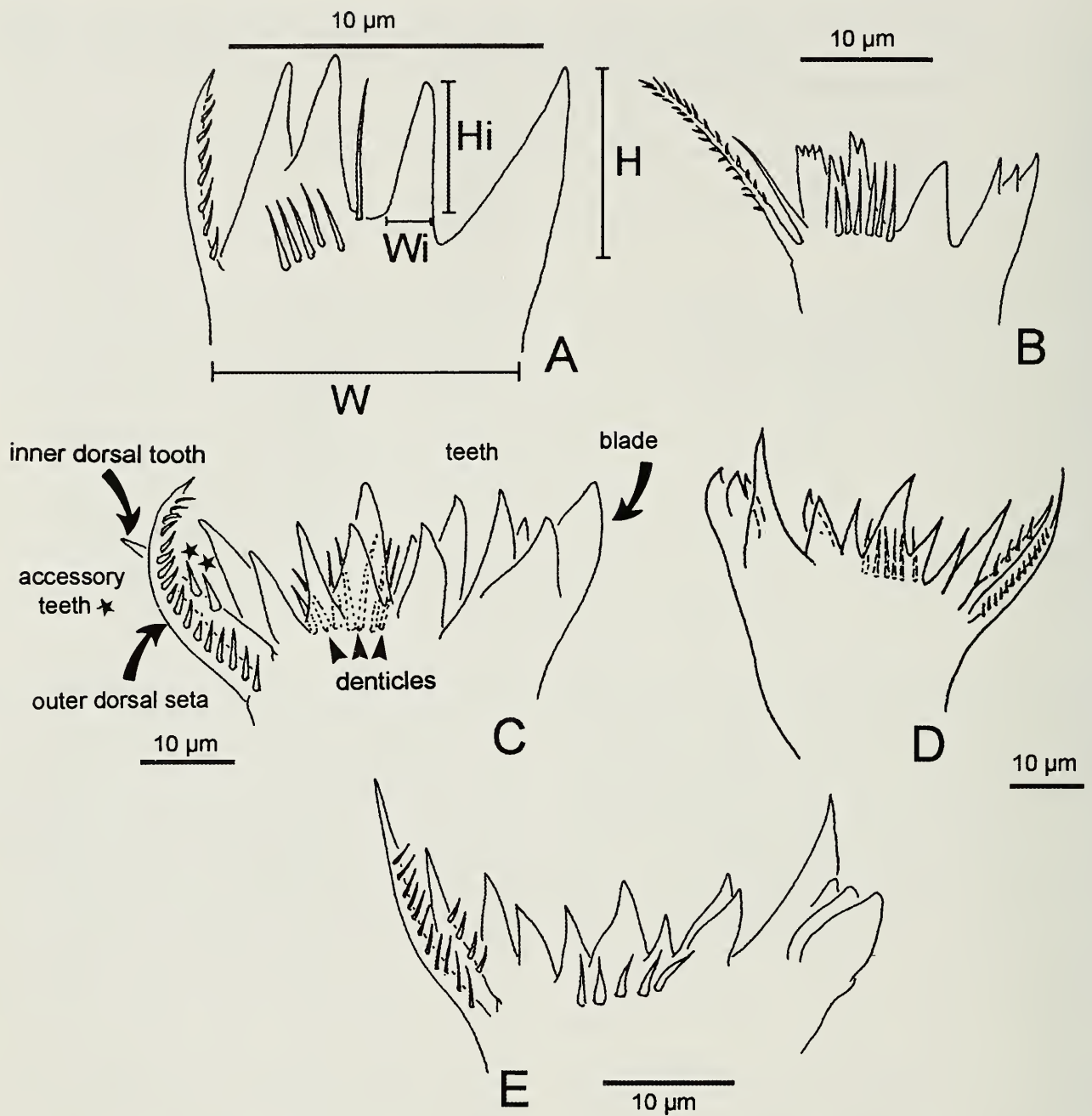


Fig. 1. Structure and nomenclature of the mandibular edge of males and females of species of *Mesocyclops* from Mexico: A) *M. yutsil* (♀), showing factors used in index formulae; B) *M. chaci* (♀); C) *M. edax* (♀), showing nomenclature of mandibular structures. Outer dorsal seta and inner dorsal tooth are proximal; blade is distal; D) *M. aspericornis* (♀); E) *M. evadomingoi* (♀).

inner tooth, can have epicuticular extensions (such as setules or as pinnate elements mostly uniserially arranged). In some species these extensions are noticeably strong, we named these structures "accessory teeth" (see Fig. 1C). In *Mesocyclops*, the distal edge of the gnathobase has a noticeably larger tooth; it can be simple (as in Fig. 1A) or formed by a cluster of two or more teeth (see Fig. 1C, E). This structure is known herein as the blade (see Fig. 1C),

but it was counted as one tooth and also is used as a reference for measurements of the other teeth. There are setiform structures along the mandible edge, arising near the base of the teeth; these are not true setae, and are named denticles for the purposes of this work (Fig. 1C). The same nomenclature was used in the descriptions of the mandibular structure.

Formulae.—The mandibular elements (teeth number, edge width, height) were

evaluated with an index based on the Edge Index (EI) proposed by Itoh (1970) for marine calanoid copepods. The original formula of this EI is as follows:

$$EI = \sum (w_i/W \times h_i/H \times 10^4) \times 1/N$$

where W is the width of the edge of the gnathobase, measured from distal tooth to proximal seta, and w_i the width of the space between each pair of adjacent teeth, respectively. Factor H is the height of the main tooth (blade) and h_i the height of each remaining tooth, respectively (Itoh 1970), and N is the number of teeth. We modified this formula substituting the meaning of w_i by the actual width of the teeth (not the space between each tooth as in the Itho's formula) and rearranged the factors. The name of the resulting value was changed herein to gnathal index (GI), the resulting formula as:

$$GI = \sum ((w_i/W \times 1/N)(h_i/H \times 1/N)) \\ \times 1000$$

where w_i is the width of each tooth, not the space between them and W is the width of the edge of the gnathobase; h_i is the height of each tooth and H is the maximum height of the blade tooth (see Fig. 1A). The first factor indicates the width of each tooth compared to the total edge width, the sum of all individual tooth widths gives an idea of the how much of edge of the gnathobase is take up by teeth. A value of 1 would imply that all the available edge is covered by teeth. However, for some species the factor figure is over 1, if teeth are arranged in more than one row. Dividing the result of this factor by the number of teeth, we obtain the average tooth width. The second factor is designed to indicate how high teeth are when compared to the highest one (the blade); dividing this product by the number of teeth provides an average tooth height. The overall product of multiplying the average height and width is an idea on how strong each tooth is in the mandible, the higher and wider, the stronger. Additionally, we formulated a mandibular size index (MSI) to quantify the length of the edge of the gnathobase as it relates to the

total body length of the specimen. This index is obtained from the following formula: $MSI = W/TL \times 100$, where W is the width of the mandible edge (in μm) and TL the length of the species (in μm) including the caudal rami. This index is expected to provide a comparative estimation on how large are the mandibles with respect to the size of the copepod. The figure obtained is a percentage, scaled to 100. The relation between TL and MSI was analyzed statistically by determining the correlation factor (r). Finally, by multiplying GI by MSI , the mandibular power index (MPI) is obtained, which provides a measure of the strength-size combination of the mandibles of each species. That is, a species with a high GI will not necessarily have a high strength-size combination, if the width of the blade is small relative to the length of the specimen (as indicated by the MSI).

Results

Material examined.—*Mesocyclops aspericornis*: 3 adult ♀♀ from small reservoir near km 90 of the highway Culiacán-Los Mochis, Sinaloa, Mexico (25°17'N, 107°47'W); 1 adult ♀ from Anapoima, Cundinamarca, Colombia (04°33'N, 074°32'W), USNM-216634; *M. brasiliensis*: 6 adult ♀♀, 2 adult ♂♂ from Sayaxché, Guatemala (16°31'57"N, 90°11'18"W). 1 adult ♀, Mantecal, Venezuela, Collection of B. Dussart, MNHN Cp 821, 1 adult ♂, Lago Valencia, Venezuela (10°10'N, 0.67°45'00"W), USNM-204662; *M. chaci*: 1 adult ♀, 1 adult ♂, Gruta Tza-Ma, Yucatán, Mexico (USNM-274244); *M. edax*, 2 adult ♀♀ from Cranes Pond, North Carolina, USA, 1 adult ♀, Cenote Viejo, central Quintana Roo, Yucatan Peninsula, Mexico, USNM-259699; *M. evadomingoi*, holotype specimen, pond at km 45 of the Jonuta-Villahermosa federal road, Tabasco, Mexico (17°58'44"N, 92°14'11"W), slides ECO-CHZ 01157 (♀), paratype ECO-CHZ 01159 (♂); *M. longisetus* s. str.: 4 adult ♀♀ from small temporal pond near Comitán city, Chiapas, Mexico

(16°09'57"N, 92°05'23"W), 2 adult ♀♀, 2 adult ♂♂, pond at Km 51 Jonuta-Villahermosa federal road, Tabasco, México (18°23'16"N, 92°47'0"W); *M. longisetus curvatus*: 3 adult ♀♀ from small pond at km 45, Jonuta-Villahermosa federal road, Tabasco, Mexico (17°58'44"N, 92°14'11"W), 3 adult ♀♀, Cenote Catedrales, central Quintana Roo, Yucatan Peninsula, Mexico, USNM-259687; *M. pescei*: 11 ♀♀, 5 ♂♂ from small pond km 45, Jonuta-Villahermosa federal road, Tabasco, Mexico (17°58'44"N, 92°14'11"W); *M. reidae*: 1 adult ♀, 1 adult ♂ from Tabano, Cuba; *M. thermocycloides*: 3 adult ♀♀, 1 adult ♂ from Pulsar, Tabasco, Mexico (17°39'10"N, 91°33'23"W), 2 adult ♀♀, 2 adult ♂♂, from small pond at km 45 of the Jonuta-Villahermosa federal road, Tabasco, Mexico (17°58'44"N, 92°14'11"W); *M. yutsil*: 2 adult ♀♀ (USNM-259843, USNM-259846) from cenote Yuncú, Yucatan Peninsula, Mexico; 1 adult ♀, Cenote Mucuyché, Yucatan, Mexico (USNM-259848).

Structure of mandibles.—The mandibular edge in this genus follows a general pattern, with a strong blade which is, in most cases, the largest and strongest one on the gnathal edge (Fig. 1). In some species such as *M. evadomingoi* (♀), *M. pescei* (♂, ♀), and *M. thermocycloides* (♀), the blade is formed by a cluster of two or more teeth. A row or rows of smaller teeth follow toward the proximal end. Teeth may be bicuspidal or multicuspidal. Teeth have a variable basal width and may have groups or rows of small denticles at their base. In some species, the inner proximal tooth is quite strong and armed with two or more internal accessory teeth (i.e., *M. edax*, *M. longisetus* s.str.). The structure of the blade showed some range of variation in the species of *Mesocyclops* studied (Figs. 1, 2). A brief description of the mandibular morphology of each species and sex examined is given below together with the percent variability of the indexes estimated; this is provided only for those species in which we could evaluate these variation. Total num-

ber of teeth includes the blade and the inner proximal tooth. GI, MSI, MPI are given in Table 1. When material was available to determine the variability of the indices, the percentage range of variation from the average is indicated in each case for the species.

Mesocyclops aspericornis (♀): Gnathobase with 10–11 wide-based teeth, all monocuspidal. Distal blade of three teeth. A single row of 6 denticles inserted near base of teeth on central part of gnathal edge. Proximal seta spinulated; inner proximal tooth with row of four accessory teeth (Fig. 1D). Variability in percent with respect to average: GSI (11.9%), MSI (8.8%), MPI (18.4%).

Mesocyclops brasiliianus (♀): Gnathobase with 8 wide-based teeth, all teeth monocuspidal. Two paired sets of denticles inserted near base of teeth on central part of gnathobase. Proximal seta slender, long, with row of setules on inner margin (Fig. 2B). Inner proximal tooth naked. Variability in percent with respect to average: GSI (14.1%), MSI (9%), MPI (5.1%).

Mesocyclops brasiliianus (♂): Gnathobase with 4 wide-based teeth, all teeth monocuspidal. Blade a cluster with two distal teeth. Two groups of denticles inserted near base of teeth on central part of gnathobase. Proximal seta short, lightly setulated (Fig. 2A). Variability in percent with respect to average: GSI (12.3%), MSI (8.7%), MPI (19.3%).

Mesocyclops chaci (♀): Gnathobase forming cluster of 3–4 wide-based teeth, proximal seta biserially pinnate. Inner proximal tooth slender, setiform, next proximal tooth tetracuspidal, next one monocuspidal, next one bicuspidal, distal monocuspidal, blade formed by a cluster of three teeth. Row of six denticles inserted near base of bicuspidal tooth on central part of gnathobase (Fig. 1B).

Mesocyclops evadomingoi (♀): Gnathobase wide, with 12 wide-based teeth, all monocuspidal. Distal cluster of three teeth partially fused to blade. Row of five den-

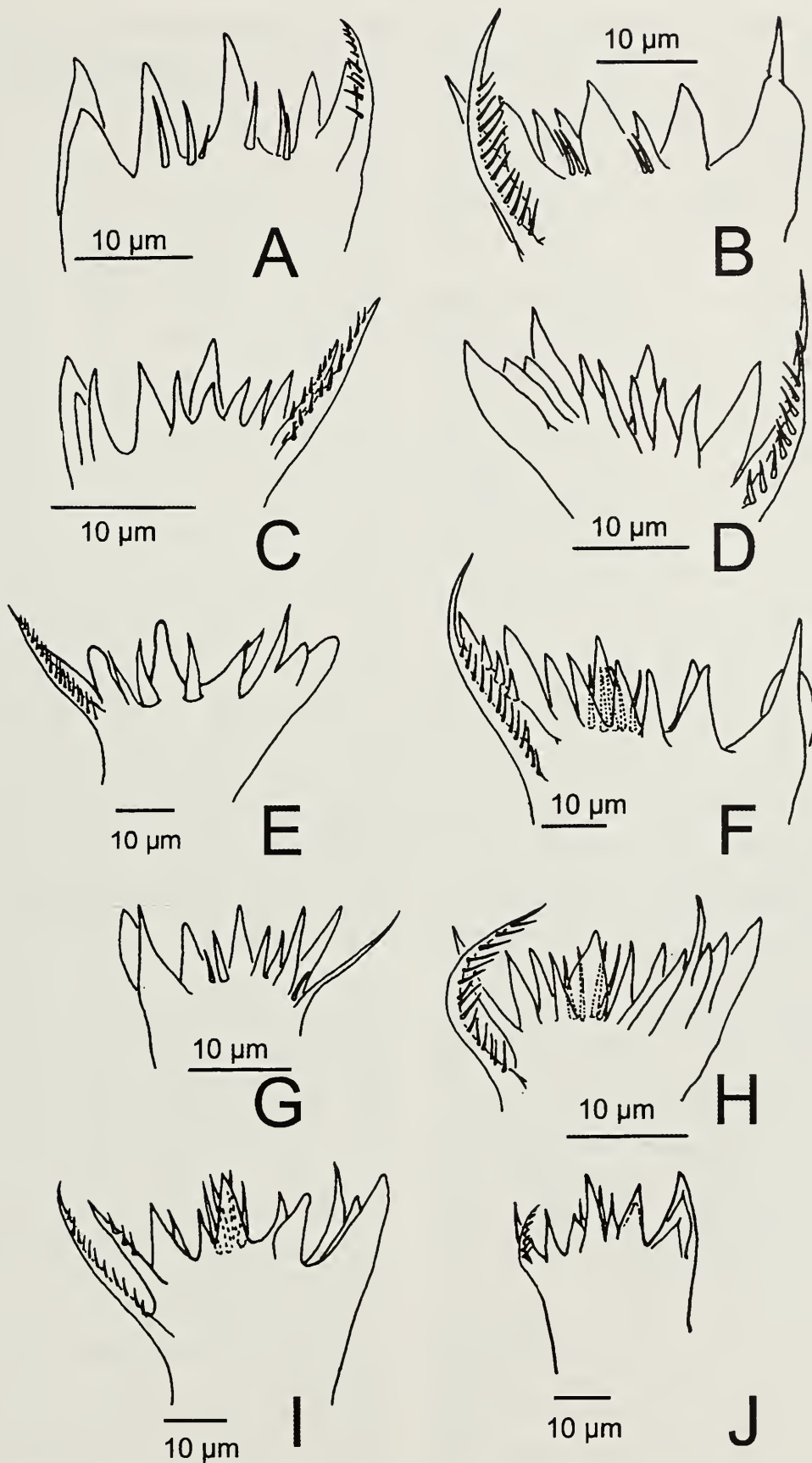


Fig. 2. Structure of the mandibular edge of males and females of species of *Mesocyclops* from Mexico; A) *M. brasiliensis* (♂); B) *M. brasiliensis* (♀); C) *M. pescei* (♂); D) *M. pescei* (♀); E) *M. longisetus curvatus* (♂); F) *M. longisetus* s.str. (♀); G) *M. thermocyclopoides* (♂); H) *M. thermocyclopoides* (♀); I) *M. reidae* (♀); J) *M. reidae* (♂).

ticles inserted near base of teeth on central part of gnathobase. Outermost proximal seta long, with uniserial row of spinules along inner margin; inner proximal tooth relatively short, with row of 3–4 secondary teeth on inner margin (Fig. 1E). Variability in percent with respect to average: GSI (4.4%), MSI (3.4%), MPI (0.3%).

Mesocyclops edax (♀): Gnathobase with 13 wide-based teeth, all monocuspidal. A single row of 6–7 denticles inserted near base of the teeth on central part of the gnathal edge. Distal cluster of three strong teeth clustering partially with blade. Proximal seta heavily spinulated along inner margin only. Inner proximal tooth with 2–3 strong accessory teeth (Fig. 1C). Variability in percent with respect to average: GSI (4.7%), MSI (2.3%), MPI (4.5%).

Mesocyclops longisetus s.str. (♀): Gnathobase with 8–10 wide-based teeth, all teeth monocuspidal. Row of five denticles inserted near base of teeth on central part of gnathobase. Proximal seta relatively long, slender, with inner row of short setules. Inner proximal tooth with three strong accessory teeth (Fig. 2F). Variability in percent with respect to average: GSI (20.6%), MSI (2.9%), MPI (22.3%).

Mesocyclops longisetus curvatus (♀): Gnathobase with 10–11 wide-based teeth, all teeth monocuspidal. Blade with blunt tip. Proximal seta relatively long, slender, with inner row of short spinules. Inner proximal tooth naked, shorter than the proximal seta (Fig. 2E). Variability in percent with respect to average: GSI (14.4%), MSI (16.4%), MPI (27.4%).

Mesocyclops pescei (♀): Gnathobase with 12 teeth, all monocuspidal. Base of teeth unornamented. Distal cluster of four teeth partially fused with blade. Proximal seta long, strongly spinulated along inner margin. Inner proximal tooth slender, naked, slightly longer than proximal seta (Fig. 2D). Variability in percent with respect to average: GSI (15%), MSI (6.9%), MPI (16.2%).

Mesocyclops pescei (♂): Gnathobase

with 11 wide-based teeth, all monocuspidal. Base of teeth unornamented. Blade partially fused to two adjacent teeth. Proximal seta relatively long, with row of spinules along inner margin. Inner proximal tooth slender, slightly shorter, with row of small, weak accessory teeth along inner margin (Fig. 2C). Variability in percent with respect to average: GSI (37.4%), MSI (15.5%), MPI (29.5%).

Mesocyclops reidae (♀): Gnathobase with 10 wide-based teeth, all monocuspidal. Base of teeth with single row of four denticles inserted on central surface of base. Distal cluster of 2–3 teeth with blade. Proximal seta relatively long, with row of short spinules along inner margin. Inner proximal tooth slender, slightly shorter than proximal seta, with three accessory teeth on inner margin (Fig. 1I).

Mesocyclops reidae (♂): Gnathobase with 9 wide-based teeth, all monocuspidal. Base of teeth with row of 2–3 denticles. Distal cluster of three teeth with blade. Proximal seta with row of short setules along inner margin. Inner proximal tooth slightly shorter, naked (Fig. 1J).

Mesocyclops thermocyclopoides (♀): Gnathobase with 12–13 wide-based teeth, all teeth monocuspidal. Row of four denticles inserted near base of teeth on central part of gnathobase. Distal cluster of 3–4 teeth partially fused with blade. Proximal seta relatively long, slender, with inner row of strong spinules. Inner proximal tooth slender, naked (Fig. 2H). Variability in percent with respect to average: GSI (10.3%), MSI (17.9%), MPI (7.6%).

Mesocyclops thermocyclopoides (♂): Gnathobase with 8 teeth, all teeth monocuspidal. Blade clustered with one tooth. Two or three denticles inserted near base of teeth on central part of gnathobase. Proximal seta relatively long, slender, naked. Inner proximal tooth absent or reduced (Fig. 2G).

Mesocyclops yutsil (♀): Gnathobase with 4 wide-based teeth, including large blade; all monocuspidal. Row of five denticles in-

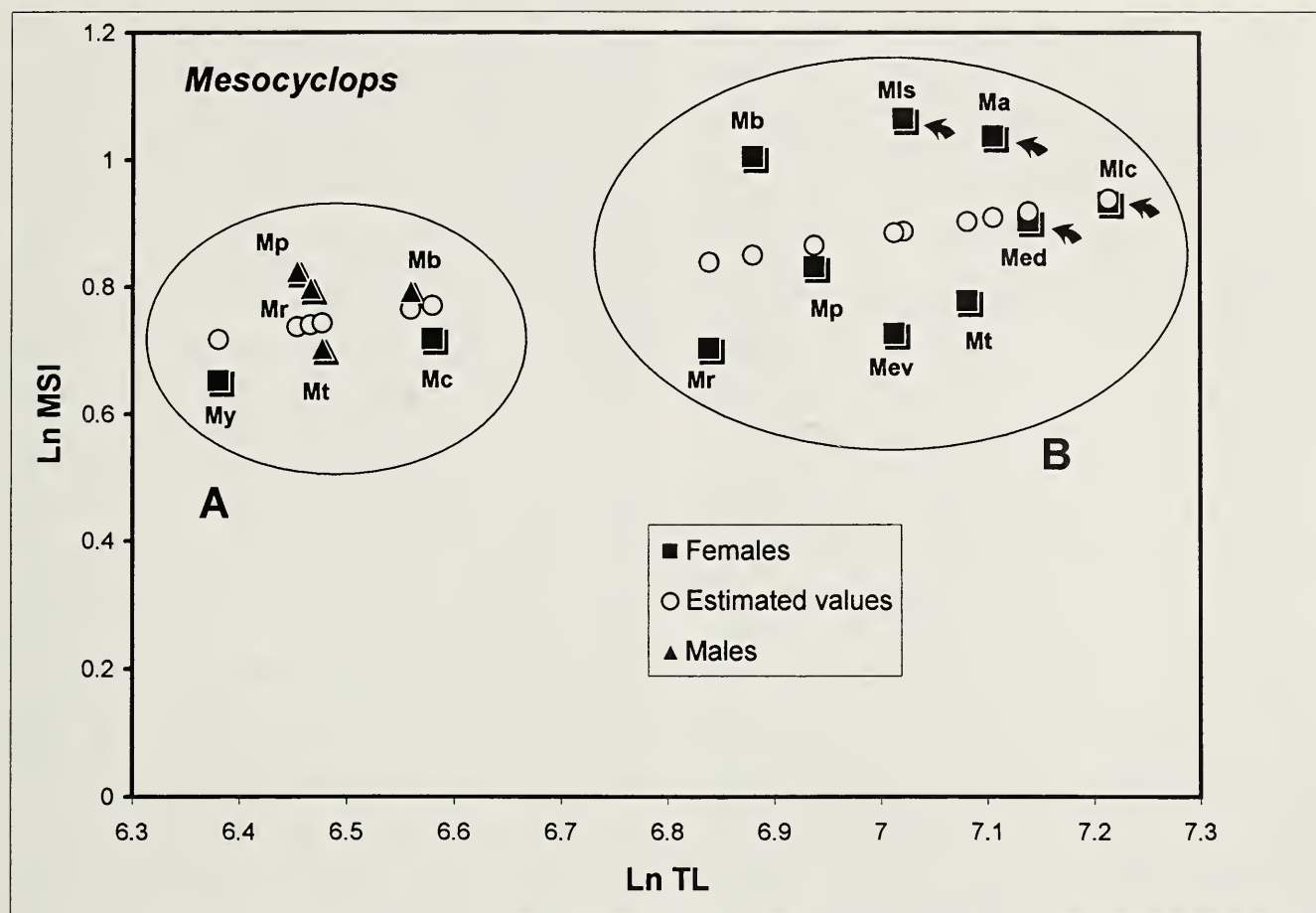


Fig. 3. MSI vs. TL logarithmic (ln) regression. Ellipses indicate two major groups with distinct features (see text for explanation) including both males (triangles) and females (squares). Arrows indicate the species with highest TL and MSI values. Species abbreviations as: Ma = *M. aspericornis*; Mb = *M. brasiliensis*; Mc = *M. chaci*; Med = *M. edax*; Mev = *M. evadomingoi*; Mls = *M. longisetus* sensu stricto; Mlc = *M. longisetus curvatus*; Mp = *M. pescei*; Mr = *M. reidae*; Mt = *M. thermocyclopoides*; My = *M. yutsil*.

serted diagonally near base of teeth on central part of gnathobase. Proximal seta relatively short, as long as adjacent teeth, with inner row of short spinules (Fig. 1A).

Discussion

The Mandibular Power Index (MPI) of species of *Mesocyclops* comparable numerical data which are presented in Table 1. The highest MPI value was that of *Mesocyclops edax*, followed by *M. aspericornis*, whereas the lowest figure was shown by the females of *M. yutsil* and *M. chaci*. Additional differences were detected between males and females of the same species. Out of the four species with both sexes evaluated, males of two (*M. reidae*, *M. thermocyclopoides*) had higher MPI values than females; females of *M. brasiliensis* and *M.*

pescei had an MPI figure higher than their males (see Table 1).

The Mandibular Size Index (MSI), size of the gnathal edge relative to body length of the specimen, yielded interesting differences among the species. Females *M. edax* have the largest mandibular edge (MSI = 4.5), followed by females of *M. aspericornis* (4.16), and females of *M. longisetus* s.str. (MSI = 3.26) (see Table 1). Females of *Mesocyclops yutsil*, *M. chaci*, and *M. reidae* have the smallest mandibles, relative to body size, of all the species examined herein (MSI = 1.92 and 2.05, respectively).

The TL vs. MSI graphic analysis, which used the logarithm (ln) of both factors, showed two distinct groups (see Fig. 3) with a positive correlation ($r = 0.598$, $p > 0.05$) which is slightly higher if only fe-

males are considered ($r = 0.62$, $p = >0.05$). Group A includes the females of most species and group B contains the four males examined and the females of *M. chaci* and *M. yutsil*. The forms with highest values in terms of MSI and TL were the females of *M. aspericornis*, *M. edax*, *M. longisetus* s.str., and *M. longisetus curvatus* (arrowed in Fig. 3). Overall, the morphology of the mandibular edge of the studied *Mesocyclops* shows a relatively wide range of variation in terms of tooth structure.

Itoh's (1970) Edge Index was modified due to the differences between the calanoid teeth/mandibular pattern and the cyclopoid pattern (see Huys & Boxshall 1991), mainly with respect to the distribution of teeth along the gnathal edge. The two main factors (width and height), when combined, provide an idea of the strength of the teeth. Then, when divided by the number of teeth (N), a quantitative measure is obtained about the strength of each tooth, which is the actual interpretation of this index for *Mesocyclops*. These figures also provide a quantitative estimation of the morphological differences found in the species examined. Although the taxonomic value of the mandible edge remains unexplored in *Mesocyclops* or in any other freshwater genus, this work reveals the many different characters with potential use for identification purposes, and that most of them can be evaluated quantitatively. Mandibles are one of the most heavily chitinized structures in the copepods; therefore, these appendages could be used to identify these crustaceans at the species level from stomach contents in trophic or ecological surveys.

The size of the body (LT) is a key factor for a copepod used in mosquito control, but one of the largest species of Cyclopidae known (*Homocyclops ater* (Herrick)) can not be used as a mosquito predator (see Marten et al. 1994b). Therefore, the use of the MSI together with the TL was considered necessary to infer the trophic habits of the species of *Mesocyclops*. The MSI vs. TL graphic (Fig. 3) yielded some interest-

ing facts: the relative size of the mandibular edge tends to be proportional to the total length of the species; males are smaller but at least in two of the males evaluated (*M. pescei*, *M. reidae*), mandibles are at least as large as those of their females. The value of males as potential predators of mosquito larvae is undetermined, although in this study the male of *M. thermocycloides* ranked higher (MPI) than the female.

The females of *Mesocyclops longisetus*, *M. aspericornis*, and *M. edax* are unique in showing a proximal seta with 2–4 strong, wide-based accessory teeth. They had the highest MSI values which, complemented with their body size (1.0–1.2 mm) suggests they are the most well-equipped species for predation within the examined group (see Fig. 3). Overall, these results agree with those of field and laboratory experiments testing the predation capabilities of *M. aspericornis* and *M. longisetus* (see Marten et al. 1994b, Suárez 1992) and of *M. edax* (Marten 1989). *Mesocyclops thermocycloides*, recorded in Honduras, Costa Rica, and Mexico, has been successfully used as a mosquito control (Marten et al. 1994a, 1994b). Only recently were the neotropical records of this species confirmed with Asian specimens (Gutiérrez-Aguirre et al. 2003). *M. thermocycloides* ranked sixth in the MSI; its size (comparable to that of *M. aspericornis* and *M. longisetus curvatus*) suggests that this species might be capable of attacking a mosquito larva. Our results on this species agree entirely with the observations obtained from experimental works by Kumar & Rao (1999a, 1999b) establishing this species as an omnivorous form feeding on rotifers, ciliates, and algae.

A second group of probably omnivorous species was found based on MSI vs TL values and MPI, i.e., the females of *M. evadomingoi*, *M. thermocycloides*, *M. pescei*, and *M. brasilianus* (see Fig. 3). MSI values range between 2.2 and 2.8; they are medium to large-sized forms (0.75 mm–1.00 mm), most with small to medium-sized mandibles (except for *M. brasilianus*,

a species with a mandible size equal to that of predator species). These omnivorous species may be capable of predation upon small prey items when conditions are appropriate to such behavior, but they may also ingest other food sources. Males of these species, some even with MSI values higher than their females, may not be able to feed on large prey (i.e., mosquito larvae) because of their relatively small size. Finally, the females of *M. chaci* and *M. yutsil* are slender, probably planktic forms (Fiers et al. 1996). In terms of size of the mandibular edge and teeth structure, these two species represent the diametral opposite end with respect to the predator group. Their mandibles are built quite differently, they probably handle algae, suspended organic matter along the water column, or even the heavily chitinized edge with these short, very solid teeth (shown by the top GI values of all the examined group) could be used to scrape off food from littoral surfaces or vegetation (if they are epibenthic forms).

According to our results, the examined species of American *Mesocyclops* exhibit a wide variation of the mandibular size and armament. We speculate that at least the morphological extremes (*M. yutsil*–*M. aspericornis*) are in correspondence with different feeding habits and prey sizes. Therefore, not all the species of *Mesocyclops* are suitable to be developed or cultured as potential biological controls of mosquitoes.

It is clear that the evaluation of the teeth strength through the GI alone could be misleading, a species with very strong teeth will rank relatively high in this index (i.e., *M. yutsil*) but this does not necessarily imply a predatorial capacity. This is why the GI should be complemented with the MSI and the MPI. A MSI value over 3 would represent a species conveniently armed for predation. We recognize, however, that the relatively reduced number of observations (see the Material examined section) is a drawback of this analysis, but still, our results seem to make sense in terms of 1) the

estimated high capacity of three well-known predator species and their consistent tendency to cluster together in the three indices used, 2) the distinction of different and even contrasting structural-morphological patterns within the genus, 3) the relation of this pattern with experimentally tested feeding habits (for predators and one omnivorous species), and 4) the relative body and mandibular size differences among the species examined herein. Of course, these patterns and estimations should be complemented with additional observations in order to have a more robust numerical analysis.

Using the detailed drawings provided in redescrptions by Dahms & Fernando (1993), we extended our results of mandibular indices to other species and genera for which feeding habits are known or inferred. *Mesocyclops leuckarti* (Claus, 1857) is a predator species (Marten 1994). The MSI estimated for this species is 4.06 and the MPI is 315.8; these values are within the range value of other predator species we have detected in this work. Although these indices were designed for *Mesocyclops*, we tested our methods on *Acanthocyclops brevispinosus* (Herrick, 1884) of the “*robustus-vernalis*” group complex (Dodson 1994). Recently, it was redescrbed by Dahms & Fernando (1997). It has a MSI of 3.82, a value which suggests predating habits. *Eucyclops conrowae* Reid, 1992), a supposedly herbivore, had a GI of 65.1, a MSI of 2.7, and a MPI of 175; these figures categorize this species within the omnivorous forms. In these or in the other instances, experimental observations will provide valuable data to find a link between the mandible structure and the feeding habits of freshwater copepods. It is probable that the differences among the species categorized here as omnivorous forms, regardless of the genus, rely mainly on the size of the potential prey they are able to capture and handle (either protozoans, planktonic algae, or insect larvae).

Literature Cited

- Deday, E. von. 1906. Untersuchungen über die Copepodenfauna von Hinterindien, Sumatra und Java, nebst einem Beitrag zur Copepodenkenntnis der Hawaii-Inseln. (Reise von Dr. Walter Volz). Zoologischer Jahrbuch, Abt. Syst., Geogr. Biol. Thiere 24(3):175–206.
- Dahms, H. U., & C. H. Fernando. 1993. Redescription of *Mesocyclops leuckarti* (Copepoda, Cyclopoida), including a study of its naupliar development.—*Internationale Revue der gesamten Hydrobiologie* 78:589–609.
- . 1997. Redescription of *Acanthocyclops brevispinosus* (Herrick, 1884) (Copepoda, Cyclopoida) from Ontario.—*Crustaceana* 70:129–144.
- Dodson, S. 1994. Morphological analysis of Wisconsin (U.S.A.) species of the *Acanthocyclops vernalis* group (Copepoda: Cyclopoida).—*Journal of Crustacean Biology* 14:113–131.
- Dussart, B. H. 1987. Sur quelques *Mesocyclops* (Crustacea, Copepoda) d'Amérique du Sud.—*Amazoniana* 10:149–161.
- Fiers, F., J. W. Reid, T. M. Iliffe, & E. Suárez-Morales. 1996. New hypogean cyclopoid copepods (Crustacea) from the Yucatán Peninsula, Mexico.—*Contributions to Zoology* 66:65–102.
- , V. Ghenne, & E. Suárez-Morales. 2000. New species of continental cyclopoid copepods (Crustacea, Cyclopoida) from the Yucatán Peninsula.—*Studies of Neotropical Fauna & Environment* 35:209–251.
- Forbes, S. A. 1890 [1891]. On some Lake Superior Entomostraca. Annual Report for the Commission of Fish and Fisheries 1887. Government Printing Office, Washington, D.C., 701–718, pls. I–IV.
- Gutiérrez-Aguirre, M., & E. Suárez-Morales. 2001a. A new species of *Mesocyclops* (Copepoda, Cyclopoida, Cyclopidae) from southeastern Mexico.—*Journal of Limnology* 60:143–154.
- . 2001b. Distribution and taxonomy of the tropical American *Mesocyclops* Sars, 1914 (Copepoda, Cyclopoida).—*Crustaceana* 74:477–487.
- , J. W. Reid & E. Suárez-Morales. 2003. An Afro-Asian species of *Mesocyclops* (Copepoda: Cyclopoida) in Central America and Mexico.—*Journal of Crustacean Biology* 23. (in press).
- Harada, I. 1931. Studien über Süßwasserfauna Formosas.—*Annotationes Zoologicae Japonenses* 13:149–168.
- Itoh, K. A. 1970. A consideration on feeding habits of planktonic copepods in relation to the structure of their oral parts.—*Bulletin of the Plankton Society Japan* 17:1–10.
- Kiefer, F. 1936. Brasilianische Ruderfusskrebse (Crustacea, Copepoda), gesammelt von Herrn Dr. Otto Schubart. V. Mitt.—*Zoologischer Anzeiger* 116:31–35.
- Kumar, R., & T. R. Rao. 1999a. Effect of algal food on animal prey consumption rates in the omnivorous copepod, *Mesocyclops thermocyclopoides*.—*International Revue of Hydrobiology* 84:419–426.
- . 1999b. Demographic responses of adult *Mesocyclops thermocyclopoides* (Copepoda, Cyclopoida) to different plant and animal diets.—*Freshwater Biology* 42:487–501.
- Marten, G. G. 1984. Impact of the copepod *Mesocyclops leuckarti pilosa* and the green alga *Kirchneriella irregularis* upon larval *Aedes albopictus* (Diptera: Culicidae).—*Bulletin of the Society of Vector Ecologists* 9:1–5.
- . 1989. A survey of cyclopoid copepods for control of *Aedes albopictus* larvae.—*Bulletin of the Society of Vector Ecologists* 14:232–236.
- , & G. Thompson. 1997. Copepod production and application for mosquito control.—New Orleans Mosquito Control Board, New Orleans, U.S.A., 42 pp.
- , R. Astaiza, R. Monje, & J. W. Reid. 1989. Natural control of larval *Anopheles albimanus* (Diptera: Culicidae) by the predator *Mesocyclops* (Copepoda: Cyclopoida).—*Journal of Medical Entomology* 26:624–627.
- , G. Borjas, M. Cush, E. Fernández, & J. W. Reid. 1994a. Control of larval *Aedes aegypti* (Diptera: Culicidae) by cyclopoid copepods in peridomestic breeding containers.—*Journal of Medical Entomology* 31:36–44.
- , E. S. Bordes, & M. Nguyen. 1994b. Use of cyclopoid copepods for mosquito control.—*Hydrobiologia* 292/293:491–496.
- Omori, M., & T. Ikeda. 1992. Methods in marine zooplankton ecology. Krieger Publishing Co., Florida, 332 pp.
- Petkovski, T. K. 1986. Zur Taxonomie des genus *Mesocyclops* G.O. Sars 1914 (Crustacea, Copepoda Cyclopoida) in der Neotropis.—*Acta Musei Macedonici Scientiarium Naturalium* 18:47–49.
- Reid, J. W. 1992. Copepoda (Crustacea) from fresh waters of the Florida Everglades, U.S.A., with a description *Eucyclops conrowae* n. sp.—*Transactions of the American Microscopical Society* 111:229–254.
- Sinh Nam, V., N. Thi Yen, M. Holynska, J. W. Reid, & B. H. Kay. 2000. National progress in dengue vector control in Vietnam: survey for *Mesocyclops* (Copepoda), *Micronecta* (Corixidae), and fish as biological control agents.—*American Journal of Tropical Medicine and Hygiene* 62:5–10.
- Suárez, M. F. 1992. *Mesocyclops aspericornis* for the control of *Aedes aegypti* in Puerto Rico and Anguilla. Pp. 151–157 in S. B. Halstead, & H. Gó-

- mez-Dantes, eds., Dengue—a worldwide problem, a common strategy. Proceedings of the International Conference on Dengue and *Aedes aegypti* community-based control. Rockefeller Foundation and Mexican Ministry of Health, Mexico City, 232 pp.
- Suárez-Morales, E., & M. A. Gutiérrez-Aguirre. 2001. Morfología y taxonomía de los *Mesocyclops* (Crustacea: Copepoda: Cyclopoida) de México. CONACYT/ECOSUR, México, 207 pp.
- , & J. W. Reid. 1998. An updated list of the free-living freshwater copepods (Crustacea) of Mexico.—*Southwestern Naturalist* 43(2):256–265.
- , J. W. Reid, T. M. Iliffe, & F. Fiers. 1996. Catálogo de los copépodos (Crustacea) continentales de la Península de Yucatán México. CONABIO/ECOSUR, 298 pp.
- Thiébaud, M. 1912. Copépodes de Colombie et des Cordillères de Mendoza.—*Mémoires de la Société Neuchateloise des Sciences Naturelles* 5: 160–175.